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Morphometrics of domestic *Panstrongylus rufotuberculatus* in Bolivia

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The trend to domesticity in Triatominae may represent a transitionary phase towards increasing vectorial importance in the transmission of Chagas disease to humans, and requires sustained entomological surveillance. Although generally considered a sylvatic species, *Panstrongylus rufotuberculatus* has been recently captured inside human dwellings in the provinces of Nor Yungas and Muñecas in the Department of La Paz, Bolivia, providing evidence of this species' ability to colonise domestic habitats. The results of previous research on domestic and sylvatic specimens of other species of Triatominae indicate that morphometrics could be used to monitor this adaptive process. The most likely cause of differences seen in the size and shape of bugs from domestic colonies of *P. rufotuberculatus* from two neighbouring villages in Bolivia is probably genetic drift rather than environmental influences. Comparison with allopatric sylvatic specimens, including the holotype of *P. rufotuberculatus*, showed a general reduction in size from sylvatic to domestic specimens.

Panstrongylus rufotuberculatus (Champion) is a widespread species of Triatominae (Hemiptera: Reduviidae) recorded from many sylvatic habitats from Bolivia northwards into Central America and Mexico (Lent and Wygodzinsky, 1979; Schofield, 1994). Adult bugs often fly into rural houses at night, presumably attracted by light, and several have been found naturally infected with *Trypanosoma cruzi*, causative agent of Chagas disease (American trypanosomiasis). Until recently, however, domestic colonies of *P. rufotuberculatus* were unknown and the species was not considered a significant vector.

In Bolivia, *P. rufotuberculatus* was first recorded from forested areas of the Alto Beni, in the Department of La Paz (Torrico, 1958). In recent years, however, there have been increasing reports of this species in rural houses of the Nor Yungas province of La Paz, including the finding of nymphs, which is evidence of domestic colonisation (Noireau *et al.*, 1994). This provides the opportunity to study the process of adaptation to domestic environments, which seems to be an increasing trend amongst several species of sylvatic Triatominae (Schofield, 1994). The aim of the present study was to analyse morphometric traits of *P. rufotuberculatus* from recently established domestic colonies, which can serve as markers for genetic differentiation of bug populations (Dujardin and Casini, 1996; Dujardin *et al.*, 1997*b*, *c*).

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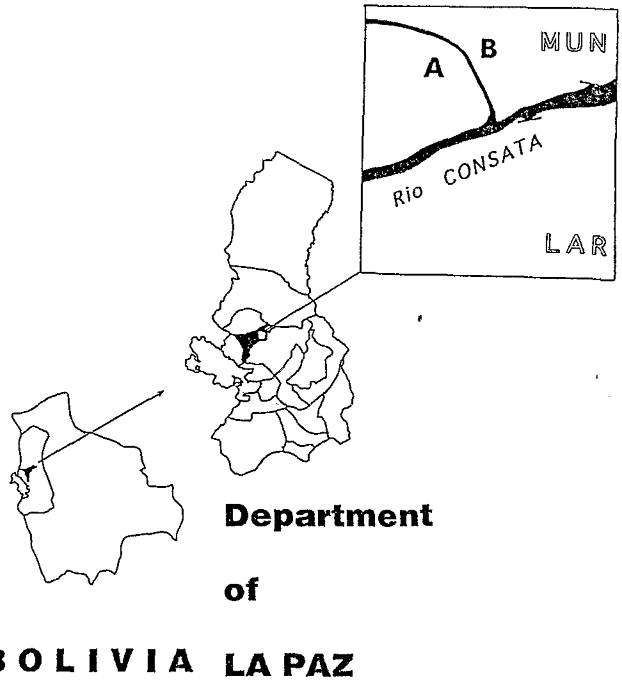

Fig. 1. Sketch map showing the location of the two collection sites in the Department of La Paz, Bolivia. A, Huayruruni; B, Nemeconi; MUN, Muñecas province; LAR, Larecaja province.

MATERIALS AND METHODS

The Insects

Nymphs and adults of *P. rufotuberculatus* were collected by hand from houses in two neighbouring localities of Muñecas province in the Department of La Paz, Bolivia (Fig. 1): Nemeconi and Huayruruni. Rectal contents of the bugs were analysed microscopically for the presence of *T. cruzi*, and adult bugs were then dissected. Heads and wings were stored dry at room temperature for morphometric analysis whereas legs and thoraces were stored at −20°C for biochemical studies. The morphometric analysis of the adult head capsules was the subject of the present study.

For comparison with sylvatic specimens, the head capsules of the four male specimens of *P. rufotuberculatus* (including the holotype) deposited in the collection of the Natural History Museum (NHM), London, were also measured. According to their labels, these specimens were collected in: (1) Campeche, Mexico (tropical rainforest; at light); (2) Paramba, Ecuador (3500 feet above sea level); (3) Jaque, Panama (sea level); and (4) Bugaba, Panama (800–1500 feet above sea level) (holotype).

Head Morphometry

By microscopy, nine measurements were taken from the head of each adult specimen, as indicated in Fig. 2. A total of 47 specimens was measured: 15 males and eight females from Nemeconi, and 12 males and 12 females from Huayruruni. All measurements from domestic bugs were taken by the same investigator at magnifications of ×50 (PO and AC) or ×25 (others). Sylvatic specimens were measured by another investigator at ×12 and ×25.

Numerical Analysis

Means and S.D. for each variable (Table 1) were compared by non-parametric univariate

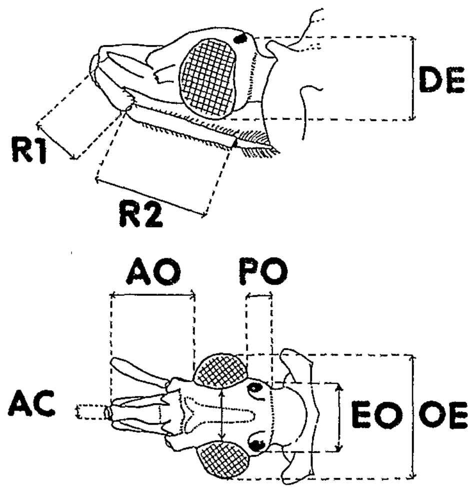

Fig. 2. Lateral and dorsal aspects of the head of an adult *Panstrongylus rufotuberculatus*, showing the morphometric measurements taken: AC (width of anteclypeus); AO (anteocular distance); DE (diameter of eye); EO (external distance between ocelli); OE (outer distance between eyes); PO (postocular distance excluding neck); R1 (length of first rostral segment); and R2 (length of second rostral segment). The inner distance between eyes (IE) is indicated but left unlabelled for clarity.

analyses (Kruskal and Wallis, 1952). To limit the overall experimental error, each comparison was tested for significance using the sequential Bonferroni test (Sokal and Rohlf, 1995).

For multivariate analysis, data were log-transformed for principal-component analysis (PCA) using the matrix of covariances. To avoid matrix singularities, one of the measures, IE (the inner distance between the eyes) was removed because it partially overlaps with another (OE, the outer distance between eyes). The male sylvatic and domestic specimens were analysed by principal-component analysis (PCA-SD) for variation in the five variables (OE, EO, AO, RC and R1; see Fig. 2) that were size-related (i.e. significantly correlated with the first principal component; see Table 3). A factorial map was then constructed for the first and second principal components to illustrate size differences between sylvatic and domestic specimens (Fig. 3). The domestic male and female specimens were compared by a further principal-component analysis (PCA-D) using the four variables (AO, PO, R1 and R2; see Fig. 2) that were positively correlated with the first principal component (see Table 3). The residuals from their regressions on the first principal component were used for size-free canonical variate analysis (SF-CVA) (Bookstein, 1989; Hutcheson *et al.*, 1995), which could be compared with size-in canonical variate analysis (SI-CVA) using all the variables. These analyses were carried out by sex and locality of the specimens, with significance checked by Wilks' statistics (Wilks, 1932). Domestic specimens were also reclassified by each CVA, and the accuracy of classification tested by kappa statistics (Landis and Koch, 1977). All calculations were made used JMP® software (Anon., 1995).

RESULTS

Infection

None of the bugs was found to be positive for *T. cruzi* infection by microscopy of rectal contents.

Univariate Analysis

Univariate comparisons of the head measurements showed differences according to ecotope, locality and sex (Table 1).

Overall, domestic females were significantly larger than domestic males, for six of the measured variables. The sexual dimorphism was more pronounced in Huayruruni (seven significant differences) than in Nemeconi (two significant differences) (Table 2).

The dimensions of the heads of the sylvatic males were generally larger than those of the domestic males (Table 2), except for the post-ocular region. In contrast, domestic specimens showed few differences between localities: the females did not differ and males differed at only one measure (Table 2).

TABLE 1

Measurements of the heads of the bugs

Group	N	OE	IE	EO	AO	PO	DE	R1	R2	AC
		*Mean (S.D) value (μm)**								
Domestic females	20	2520 (80)	1440 (40)	1560 (<40)	1880 (80)	680 (40)	1560 (80)	1160 (<40)	2560 (80)	400 (<20)
Domestic males	27	2560 (80)	1320 (40)	1520 (40)	1800 (40)	640 (40)	1560 (40)	1120 (<40)	2440 (80)	380 (<20)
Sylvatic males	4	2860 (130)	1300 (<65)	1625 (65)	2080 (195)	390 (130)	1820 (130)	1170 (130)	2730 (260)	390 (65)
Huayruruni females	12	2520 (80)	1440 (40)	1560 (<40)	1880 (80)	700 (20)	1560 (40)	1160 (<40)	2560 (80)	400 (<20)
Nemeconi females	8	2560 (40)	1400 (40)	1520 (<40)	1880 (80)	660 (60)	1600 (80)	1160 (<40)	2480 (40)	400 (<20)
Huayruruni males	12	2520 (80)	1320 (40)	1520 (<40)	1760 (40)	640 (40)	1520 (40)	1160 (<40)	2440 (40)	380 (<20)
Nemeconi males	15	2560 (40)	1320 (40)	1520 (<40)	1800 (80)	640 (40)	1560 (40)	1120 (<40)	2440 (80)	380 (<20)

* See Fig. 2 for measurements taken.

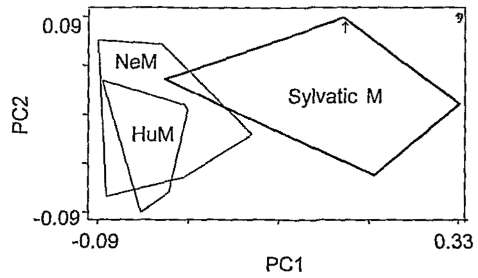

Fig. 3. Projection of male *Panstrongylus rufotuberculatus* on the first (PC1) and second (PC2) principal components using log-transformed values of OE, EO, AO, AC, R2 and AC. These variables were significantly correlated with PC1, which represents 67% of the total size variation. Thus low values of PC1 indicate relatively small size. Polygons enclose specimens of each group: NeM (Nemeconi males); HuM (Huayruruni males); and Sylvatic M (male specimens from the Natural History Museum in London). The position of the holotype is indicated (↑).

Multivariate Analysis

In both principal-component analyses (PCA-SD and PCA-D), the first principal component was compatible with a multivariate variable of size (Table 3). Figure 3 therefore indicates a general reduction in size from sylvatic to domestic specimens, as suggested by the univariate comparisons. Size variation could be removed for the comparison of domestic specimens between localities; specimens from the two localities, although not well differentiated by univariate analysis, became distinct entities after multivariate analysis (Fig. 4). Size-in and size-free CVA were both highly significant ($P < 0.001$) and allowed satisfactory reclassification of the domestic specimens (81% agreement by SI-CVA, kappa = 0.74; 60% agreement by SF-CVA, kappa = 0.45) (Table 4). Not surprisingly, better reclassification was achieved by pooling sexes, with 85% agreement and a kappa value of 0.70 for SF-CVA or SI-CVA (detailed results not shown).

DISCUSSION

Panstrongylus rufotuberculatus is widespread in sylvatic ecotopes and particularly associated with terrestrial and sub-canopy, forest vertebrates. Lent and Wygodzinsky (1979) noted that the species is 'attracted to light ... and known to occur in houses' but added that 'there is no evidence that it breeds there'. In the last 5 years, however, this species has been found in and around houses in Colombia (J. Moreno, unpubl. obs.), Ecuador (C. J. Schofield, unpubl. obs.), Mexico (P. M. Salazar, unpubl. obs.), and in two different provinces of Bolivia (Noireau *et al.*, 1994; present study), indicating an adaptive trend towards greater association with humans. A similar trend has been observed in other species of Triatominae (Carvalheiro and Barreto, 1976; Silveira *et al.*, 1984; Tibayrenc and Le Pont, 1984; Garcia Zapata *et al.*, 1985; Alencar, 1987; Dujardin *et al.*, 1991) and may represent a transitional phase towards increasing vectorial significance (Schofield, 1988; Schofield and Dolling, 1993). Successive steps in the transition have been described (Zeledón, 1974; Barreto, 1979; Schofield, 1988). The final step, observed in *Triatoma infestans* (Dujardin *et al.*, 1987) and suspected in *Rhodnius prolixus* (Schofield and Dujardin, 1997), involves incipient separation from the original sylvatic populations, as evidenced by metric and genetic comparisons (Carlier *et al.*, 1996; Dujardin and Casini, 1996; Dujardin *et al.*, 1997*a*, *b*).

The presence of nymphal stages of *P. rufotuberculatus* in the houses examined in the present study and by Noireau *et al.* (1994) is evidence that this species breeds in the houses. However, as quantitative data on the abundance of *P. rufotuberculatus* in domestic habitats are lacking, the degree of 'domesticity' of this species cannot yet be determined accurately. Sylvatic specimens of *P. rufotuberculatus* have been found infected with *T. cruzi* in the Nor Yungas province of Bolivia (G. Vargas, unpubl. obs.), confirming their susceptibility to infection. Thus the apparent absence of infection in the present specimens and those found by Noireau *et al.* (1994) lends

TABLE 2

Univariate, Kruskal–Wallis, pairwise comparisons

	Comparison between:					
	Sexes, by locality			Localities, by sex		
*Variable**	*Huayruruni*	*Nemeconi*	*Huayruruni and Nemeconi*	*Female*	*Male*	*Domestic and sylvatic males*
OE	0.7970	0.1911	0.6144	0.2601	0.0168	0.0015†
IE	0.0001†	0.0012†	0.0000†	0.1947	0.7806	0.4356
EO	0.0243†	0.4628	0.0227	0.0452	0.7258	0.0027†
AC	0.0094†	0.0029†	0.0000†	0.4528	0.6592	0.0257
PO	0.0016†	0.0088	0.0025†	0.0560	0.7985	0.0012†
DE	0.1292	0.2418	0.1670	0.0316	0.0032†	0.0018†
R1	0.0130†	0.1062	0.0047†	0.9682	0.1507	0.4610
R2	0.0004†	0.0834	0.0001†	0.0140	0.4437	0.0307
AC	0.0038†	0.0579	0.0008†	0.1330	0.5987	0.0419

* Head measurements (see Fig. 2).

† Found to be significantly different, after sequential Bonferroni test ($P < 0.05$).

TABLE 3
Results of the principal-component analyses, showing the coefficients of the first principal component and the correlation between this component and various head measurements

*Sylvatic and domestic males**				*Domestic males and females†*			
Variable‡	*Coefficient*	*Correlation*	P	*Variable‡*	*Coefficient*	*Correlation*	P
OE	0.40	0.86	0.0000	AO	0.72	0.79	0.0000
EO	0.23	0.56	0.0011	PO	0.48	0.69	0.0000
AO	0.57	0.85	0.0000	R1	0.57	0.55	0.0000
R2	0.43	0.88	0.0000	R2	0.25	0.61	0.0000
AC	0.52	0.81	0.0000				

* First and second principal components contributed 67% and 15% of total variation, respectively.
† First and second principal components contributed 42% and 30% of total variation, respectively.
‡ Head measurements (see Fig. 2).

TABLE 4
Classification to locality, by size-in and size-free, canonical variate analysis

	Huayruruni		*Nemeconi*		
	Females	*Males*	*Females*	*Males*	*Total predicted*
SIZE-IN*					
Huayruruni females	10	0	2	0	12
Huayruruni males	1	10	0	1	12
Nemeconi females	1	0	5	1	7
Nemeconi males	0	2	1	13	16
Total observed	12	12	8	15	47
SIZE-FREE†					
Huayruruni females	10	5	1	2	18
Huayruruni males	1	5	1	1	8
Nemeconi females	0	0	4	3	7
Nemeconi males	1	2	2	9	14
Total observed	12	12	8	15	47

* Observed agreement (81%) is greater than expected by chance [26%; $P = 0.000$; kappa = 0.74, representing 'substantial agreement' according to Landis and Koch (1977); $Z = 8.60$].

† Observed agreement (60%) is greater than expected by chance [26%; $P = 0.000$; kappa = 0.45, representing 'moderate agreement' according to Landis and Koch (1977); $Z = 5.36$].

support to the idea of domiciliation as a recent event, as the insects become associated with uninfected humans as their principal host. The strong sexual dimorphism shown by the present morphometric measures (Table 2) can also be interpreted as evidence for recent domiciliation, since a progressive reduction in sexual dimorphism amongst domestic and laboratory populations has been observed in other species, such as *Tri. infestans*, *R. prolixus* and *P. megistus* (J. P. Dujardin, M. Steindel, T. Chavez and C. J. Schofield, unpubl. obs).

In all documented cases, domestic triatomine populations present genetic differ-

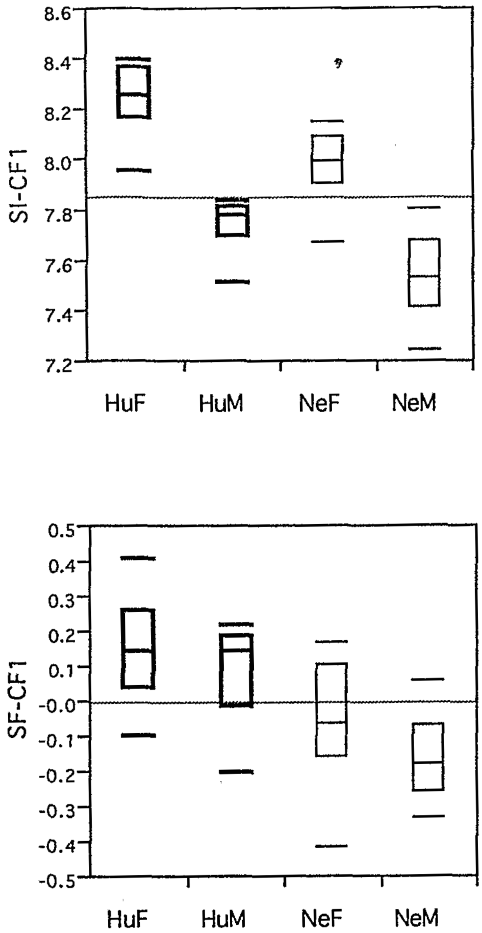

Fig. 4. Quantile plots showing the distribution of individuals of different groups of *Panstrongylus rufotuberculatus* along the first canonical factor (CF1) following canonical variate analysis (CVA) of characters OE, AO, PO, DE, R1 and R2 for size-in CVA (SI-CF1), and after size-free CVA on the residuals of the separate regressions of AO, PO, R1 and R2 on the first principal component for domestic males and females (SF-CF1). Each box shows the group median separating the 25th and 75th quartiles, with the 10th and 90th quartiles shown as short lines above and below the box. All pairwise comparisons were significant ($P < 0.001$). In the SI-CVA, males and females are separated by the total response mean (horizontal line). In the SF-CVA, the total response mean tends to separate the localities. HuF and HuM, females and males from Huayruruni, respectively; NeF and NeM, females and males from Nemeconi, respectively.

ences compared with their sylvatic conspecifics (Carlier *et al.*, 1996; Dujardin and Casini, 1996; Dujardin *et al.*, 1997*a*; Schofield and Dujardin, 1997), resulting mainly from demographic adaptations in the stable habitats offered by domestic environments. Domestic habitats offer greater protection from climatic extremes and opportunistic predators, and allow simplification of host- and mate-finding behaviours and reduction in adult dispersal (Schofield, 1988). Population densities increase and become mediated by strong density-dependent interactions with the vertebrate hosts (Schofield, 1985), increasing the level of inbreeding within the domestic colony. This, combined with founder effects, can reduce the level of genetic variability within a domestic population (Dujardin *et al.*, 1997*c*) and this can be reflected in morphometric characters (Dujardin *et al.*, 1997*a*). The most striking example is the reduction in mean size of domestic specimens compared with sylvatic ones (Harry, 1994; Dujardin *et al.*, 1997*a*, *b*; see Fig. 3), which is also seen amongst Triatominae reared over successive generations in the laboratory (Szumlewicz, 1976; Zeledón, 1981).

The present analysis also shows that metric differentiation is occurring between domestic populations of *P. rufotuberculatus* from neighbouring localities, and that this differentiation is significant even when size variation is discounted. Removal of size as a differentiation factor is intended to reveal patterns of variation that would be less influenced by environmental factors (Claridge and Gillham, 1992; Hutcheson *et al.*, 1995) and is particularly useful for studies of geographical variation where ecological, climatic or altitudinal differences are apparent. In the present samples, there was no obvious evidence for such differences, but the river separating the two localities (Fig. 1) may act as a mechanism of physical separation between the two populations. The differences between the two *P. rufotuberculatus* populations may be attributed primarily to genetic drift rather than to environmental influences. The revelation of the resultant structuring of the populations by morphometry indicates that further studies on the dynamics of the domiciliation of *P. rufotuberculatus* would be useful.

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